PREFERENTIAL AND COMPULSORY BREEDING PLACES OF *AEDES (STEGOMYIA) AEGYPTI* AND THEIR LIMITS

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Of course, the one absolute material requisite, material as distinguished from conditional requisites as temperature, etc., for the breeding of mosquitos of all kinds and in every place is *water.* Fruitful oviposition of this insect then in nature takes place only in relation to water; present at the time of oviposition for such as deposit their eggs only in water; or water in the future for such as deposit their eggs in places free from water, but which will be covered by it at the proper time for them to hatch.

Given water then, in *esse* or in *posse,* it is common knowledge that some species, even some genera, of mosquitos show decided choice in the nature of the places they select for oviposition and, where such places are available, use them to the exclusion of other collections of water, or at least so much more frequently that other places are not a serious factor in the propagation of this mosquito. Nevertheless, we sometimes find that when breeding-places of the preferred kind are *not* available, this mosquito will deposit eggs in other collections of water, although it may be not in all classes of such collections.

The class of breeding-places first mentioned—*i.e.,* those utilized for oviposition when all kinds are available, we may call the *preferential breeding-places,* or the *breeding-places of election,* for the mosquito in question. The second kind—*i.e.,* those in which

eggs are deposited when, and only when, breeding-places of election are not available, may be as properly called *compulsory breeding-places* and naturally the places in which, in nature, eggs are not deposited even when they are the only collections of water available, are beyond the natural limits of even compulsory breeding-places and from the last two we may be able to determine the limits of breeding for this mosquito in nature.

Note here that when we speak of oviposition or of breeding in any place or class of place, we mean oviposition or breeding sufficient to be a serious factor in the propagation of this mosquito. When less than this it is considered negative. This is, of course, rather the view-point of the sanitarian than that of the entomologist, yet for the sanitarian it is quite consistent. In *Anopheles* surveys we grade breeding-places as ' of sanitary importance ' and ' of no sanitary importance,' and disregard the latter. In yellow fever campaigns we count our work complete when the production of *Stegomyia* is so reduced that yellow fever cannot be kept up by them, although a minimal breeding may still be going on. So the occasional finding of a few larvae of a certain mosquito in places usually free from them does not justify our putting such places in the same class with those in which larvae are habitually found in numbers. In sanitary matters, and I confess that I am inclined to look at mosquitos from a sanitary standpoint, no one cares about *a* mosquito. It is only when zeros accumulate behind them and they show as hundreds, thousands, or ten thousands that they become important—to the sanitarian, I mean.

What we have said of the relation of oviposition to the different classes of possible breeding-places may be true of all kinds of mosquitos ; it is true of many kinds, but I am confining myself here and now to one : *Aedes* (*Stegomyia*) *aegypti**—the known vector of yellow fever and dengue. I had purposed to take up the same question about some species of *Anopheles*, malaria vectors, but this would have made this article entirely too long,—a book not a paper.

For this mosquito, it is a matter of common knowledge that its breeding-places of election are collections of water in artificial (man-made) containers, or things that simulate them : wood, cement, stone and brick being preferred to metals as the material for such

* = *Stegomyia fasciata*, Fabr. Editors.

containers and wood preferred to cement. Calabashes have seemed to be especially attractive to them. Yet long ago my attention was called to the fact that these conditions of breeding, although usual, were not obligatory and, if lacking, could be substituted by others. I was in Panama City in the last part of November or very early in December of 1905, and was there inspecting the *Stegomyia* work. The man immediately in charge was a very capable one, and we visited together a number of premises, houses and patios. In all, the *depositos* of water kept for domestic use were protected against access of mosquitos. Cisterns, *tinajas* and *ollas*, all were either empty or covered, some with wire-netting, some with cloth tied on and some with well-fitting, solid covers; no water in any of them was accessible to mosquitos. Of a considerable number of premises he had inspected before I came, he reported all as being negative for larvae and in none that I examined with him could I find larvae or pupa-casts floating on the surface ; in large collections of water the latter show up far more readily than larvae themselves.

Yet in one place I was able to show him *Stegomyia* larvae, possibly ten or a dozen, and maybe twice as many, taken with a tea-spoon from a rot-hole in a tree, small ones, in the little collections of water in the axils of the leaves of some ornamental plants in the patio—a species of Colocasia. Guessing the cause for the oviposition in these places, I directed him to place, and assisted him in placing, a number of calabashes, *ollas*, and other containers of water in shady and partly dark places about the house and patio, with instructions to empty them every Saturday at the weekly inspection. The result was successful: not only was this patio free from larvae for the next three or four Saturdays when I inspected it, but I am persuaded that neither this inspector nor any of his men ever failed to examine and to provide for the elimination from any other patio of all such breeding-places as those in which we had found these larvae.

As we had found practically all of the *depositos* of water—the preferential breeding-places of this mosquito—inaccessible to it in the vicinity in which we had found the larvae just mentioned, and had not found larvae in rot-holes in trees or the axils of Colocasia leaves elsewhere, it is fair to believe that the places in which larvae were found in this patio were breeding-places of compulsion, used

only because none more suitable were available and this seemed to be, to an extent, confirmed by the result of making suitable breeding-places accessible.

It may be noted here that while we had already occasionally found *Stegomyia* larvae in the small collections of water in the axils of the ornamental Colocasias, yet we had come to regard them as of minor sanitary importance, as so small a proportion of them developed into imagos. This, indeed, seemed to be generally true of the compulsory breeding-places of this mosquito. Her progeny seemed to have a much better chance of reaching maturity in the breeding-places of election than in those she utilized only when these were not to be had. This may not be without exception, but the one exception which I have seen reported involves an artificial condition and is not pertinent to our subject.

What are the limits to the compulsory breeding-places of this mosquito ? On the Isthmus of Panama we did not find its larvae in marshes nor in seepage out-crops—so favourite a place for *Anopheles*—nor in sluggish streams and never in a street gutter, nor a roadside puddle, except when we were reasonably sure that they had been washed in from some other place, as from an overflowing cistern or a sagging house-gutter, and this was true whether more suitable breeding-places were available or not. In other words, such places were beyond the natural limits of breeding—complete breeding, from oviposition to imago—of this mosquito on the Isthmus of Panama.

Is this true everywhere, or, as happens sometimes with other mosquitos, is there a regional variant to this part of its biology ? Some years ago Francis, of the U.S. Public Health Service, as a result of his observations for some three years in and about Mobile, Ala., stated that ' larvae of this mosquito have not been found in any collection of water the bottom of which was of mud.' As intended, ' not in mud-puddles,' this seems correct and would be so accepted, I think, by all of you. As expressed, it doubtless was correct, anyway. The implication, however, that this was a general rule and that the mud bottom of a collection of water was the factor which determined that *Stegomyia* should not breed therein is erroneous. During 1920 and 1921 in Payta, Sullana, Piura, Catacaos, and in practically every other town in Northern Peru

which we examined, we found *Stegomyia* breeding and breeding freely, in the great *botijas*, or *tinajones*, used to store water in that country, although their bottoms were generally covered with mud, from six to ten inches deep. Very evidently, mud at the bottom of the water in no wise prevented their breeding in it.

Admitting that we have not found them breeding completely in mud-puddles, what are the factors which prevent this ? I think we can name one of them, and possibly the determining one. At Catacaos, a town of about 40,000 people in Northern Peru, where we had yellow fever in 1919 and 1920, there were many wells, say from 100 to 200. They were merely holes dug in the ground from six to twelve feet deep according to the depth of the ground water. We never found *Stegomyia* larvae in these wells, even when breeding was fairly well-controlled in the artificial containers in their neighbourhoods. Plenty of larvae of other mosquitos, but none of *Stegomyia*. At Casa Grande, also in Northern Peru but further south, in every house of a skilled employee there was a well and we found *Stegomyia* larvae in exactly 100 per cent. of these wells ! Why this difference ? Could it be because the wells at Casa Grande were in houses occupied by men while those at Catacaos were in the open ? It did not seem so, because the wells for general service at Casa Grande were out of doors and all that we examined, some eight or ten, showed *Stegomyia* larvae, although fewer than those in the houses. There was another difference between the wells at the two places besides their locations in, and not in, houses. Those at Casa Grande were lined with brick and cement, while those at Catacaos were unlined, simply dug in the clay. In Chiclayo, too, situated between the two places, there were a number of wells, some lined and some unlined. In none of those unlined which we examined did we find *Stegomyia* larvae ; in none of those lined, whether with wood or with brick and cement, did we fail to find them !

Really this explanation had been anticipated. Anyone who has seen the oviposition of this mosquito standing just at the edge of the water, sometimes on the water, sometimes on the container, sometimes partly on both water and container, would naturally guess that the physical nature of the sides of the container *at the water's edge* might well be a factor in her choice of a place for oviposition ; while, unless it affected the quality of the whole body of water, the nature of the bottom would be unknown to her.

After considerably more observation on this point in Peru by Hanson and by Dunn and their men and much inquiry, verbal and by letter, of men doing *Stegomyia* control work in other countries : Mexico, Yucatan, Central America, Panama and Colombia, I felt myself justified in presenting this formula, modelled on that of Francis, as limiting the breeding-places of this mosquito :

' We have not found this mosquito (Aedes (Stegomyia) aegypti) breeding, in nature, completely, that is, from oviposition to imago, in any collection of water, all the sides of which at the water's edge were of mud.'

It was thus given out in a lecture to the Laboratory Class of Officers of the U.S. Public Health Service in Washington in the Spring of 1923, and, a little later, to the class at the School of Hygiene and Public Health of The Johns Hopkins University in Baltimore. As expressed it was correct ; neither myself nor anyone of whom I had inquired had ever seen *Stegomyia* breeding in the places excluded by this formula. Even the implication was logical and I then thought correct, yet I have recently learned that, taken as a universal formula, it is not.

Last September I received, through the International Health Board of the Rockefeller Foundation, copies of official reports sent them from the British Colonial Office of the yellow fever epidemics of 1922 and 1923 in British West Africa. Among these epidemics was one at Salt Pond on the Gold Coast, small but virulent, as African yellow fever has usually proved to be. In the report on this it was stated that the principal source of *Stegomyia aegypti* at this place was the lagoon and the tracks in the mud around it of the men and boys who go bathing there. This production was stated to be large and to be uncontrollable except by a major engineering project. As illustrating the amount of this breeding, the reporter stated that in one collection of water (in this mud) of about ten inches square, characterized by him as ' a typical *Anopheles* breeding-place,' the larvae were so abundant that ' they nearly filled the saucer in which they were dipped up ' and it was added that these larvae developed into imagos of *Stegomyia aegypti* and *Culex fatigans*.

The writer of this report, Dr. Lorena, and his immediate superior, Dr. Watt, both officials of the Sanitary Service of the Colony, ascribed this breeding ' in such unusual places ' to the complete

elimination of the usual breeding-places from the town and its environment.* This, of course, would make the breeding of *Stegomyia aegypti* in and about the lagoon a compulsory breeding, there being no more suitable place available. Yet there are other reports, previous to the one quoted, implicitly accusing the Salt Pond Lagoon and its environment of producing *Stegomyia aegypti* normally—*i.e.*, when there had been no interference with their normal breeding-places. That of Drs. Horn and Tytler (Oct. 16, 1920), made in connection with the Yellow Fever Commission of the International Health Board of the Rockefeller Foundation of 1920—the one on which Gorgas was serving when he died—implies the production of *Stegomyia* in and about this lagoon, as it suggests the canalization of this lagoon as affecting the prevalence of yellow fever in Salt Pond. It also states that the same conditions exist at Seccondee and other places on this coast as at Salt Pond. In some of the reports, too, of the British West African Yellow Fever Commission—the last I saw were, I think, of 1913—and the papers transmitted with them, there were also recommendations for the abolition of this lagoon and cure of the mosquito breeding conditions around it, on account of their effect on the propagation of yellow fever at Salt Pond.

Be this as it may, neither Le Prince nor myself nor any one of the many whom I have consulted have ever seen, in the Americas, *Stegomyia* breeding, from oviposition to imagos, in mud-puddles. Nor have either of us even seen this mosquito breeding anywhere in anything like the profusion implied in this report. *Culex fatigans*, yes; *Stegomyia*, never. It is a pity the reporter did not give the proportion of the two kinds of imagos developed from his pool in the mud.

Nevertheless we cannot, on this account, reject this report as erroneous. I have seen too much of what, I suppose, may be called 'regional variation in the biology of mosquitos' to refuse credence to a well-attested statement about them, as I consider this to be, simply because it is not in accordance with my own observations made in an entirely different region. And, while I would greatly like to examine for myself the breeding of this mosquito in and

* Why, knowing this, the 'usual breeding-places' in the town and its vicinity were not at once re-established one cannot imagine. Knowing where they were these could have been easily controlled; the breeding about the lagoon had been reported as 'uncontrollable.'

about this lagoon at Salt Pond, yet I feel that we must accept the statements of fact as given in the report quoted. Without denying it I am, however, less inclined to accept the breeding of *Stegomyia aegypti* in and about the lagoon at Salt Pond *as its normal breeding there—i.e.*, as taking place when water in artificial containers was available to them for oviposition, because (1) the evidence for it that I have seen is implied rather than direct and is less in detail, (2) it seems to me antecedently more improbable, and (3) the characterization of these places, the lagoon and the tracks around it, in Lorena's report, as 'unusual breeding-places' for this mosquito, used only because the usual ones in the neighbourhood had been eliminated.*

In any case, however, we must change the formula just given you by limiting it to the Americas. And I am entirely willing to do this because all that I know of *Stegomyia* breeding at first-hand is its breeding in the Americas. Our formula should then read:

'*In the Americas* we have not found this mosquito, *Aedes* (*Stegomyia*) *aegypti*, breeding, in nature, completely, from oviposition to imago, in any collection of water all the sides of which at the water's edge were of mud.'

This is not only correct as expressed, but its implication that collections of water in the Americas under the conditions specified are not found breeding *Stegomyia* in nature is, I am inclined to think, correct also. For, since the receipt of the West African reports mentioned, I have been in communication, in reference to the breeding of *Stegomyia aegypti* in puddles, with a number of men whom I know and who are working, or have been working, in the Americas, for the elimination of yellow fever: with White, Scannell, Walcott and others in Brazil; with Hanson and Dunn, an entomologist, in Colombia; with Caldwell, Connor, Scannell and Houle in Mexico and Yucatan and with Connor in the Guianas, and no one has, so far, reported having found *Stegomyia* breeding in nature completely in mud-puddles and a number report directly to the contrary. I think then that, for the present at

* After the reading of this paper the writer had opportunity to talk to Dr. A. E. Horn, to whose report of 1920, made jointly by himself and Dr. Tytler, allusion has been made. Dr. Horn stated that he had not seen larvae of *Stegomyia aegypti* in the Lagoon at Salt Pond, nor in the puddles adjacent thereto, nor had he seen them in similar places at Seccondee. The inference then drawn from the Report of Drs. Horn and Tytler, although logical, was incorrect.

least, the implication of our modified formula, that complete breeding of *Stegomyia* in mud-puddles does not, in nature, occur in the Americas may be accepted. It is supported by a considerable amount of evidence ; negative evidence, indeed, but from the nature of the question no other kind is here possible. Is it enough—negative evidence is convincing in proportion to its mass—to justify us in asserting that, in the Americas, mud-puddles are beyond the limits of natural *Stegomyia* breeding—even of natural compulsory breeding ? I think so, but we should know when the work in Brazil is finished.

At any rate, there seems to be a difference in the limits of the natural compulsory breeding-places of this mosquito in the Americas and at Salt Pond and, it may be, in other places in West Africa. Possibly the biology of the African strain is less rigid than is that of ours ; that it can adapt itself to conditions which the American strain is unable to meet. Well was it for us that this last was true ! Had the Salada and all the puddles about Guayaquil produced *Stegomyia*, the elimination of yellow fever from that city had been more difficult even than it proved. So if the conditions of breeding as reported at Salt Pond are general in West Africa, the elimination of yellow fever therefrom will be decidedly more difficult than if the limits of the breeding of this mosquito, both normal and compulsory, were there the same as we have found them to be in the Americas.

Very obviously, then, the utilization by *Stegomyia aegypti* of breeding-places other than those of election is of decided importance to the sanitarian. It makes its control more difficult than if only the latter were used. If, as at Salt Pond, one must control its production not only from artificial containers in the town, but from mud-holes and ponds as well, the difficulty may be many-fold greater than if the first only were involved. And this difficulty might be *very* greatly increased if this adaptability of the insect to breeding in what are now abnormal places should prove to be a characteristic which can be cultivated and increased by practice, as has apparently happened with at least one characteristic of *Anopheles maculipennis*.*

It would seem advisable then so to plan our methods of *Stegomyia* control, as to limit as much as possible the use of compulsory breeding-places by this mosquito. This depends on the facilities

* The development of a preference for the blood of domestic animals over that of man in these mosquitos in certain parts of France and Denmark.

available for oviposition. As long as the mosquito has easy access to a sufficiency of breeding-places of election, she will not seek to deposit eggs in any other. *It may be advisable then to provide her with such breeding-places of election.*

Does to provide suitable breeding-places for, and easy of access to, this mosquito, of which we are trying to rid ourselves, seem a paradox? I have been asked (about *Anopheles*, however) if I 'wished to encourage them to breed?' Not exactly, but we don't care whether they breed or not, *provided there be no production.* Eggs, larvae and pupae are absolutely innocent, and if breeding is stopped short of their final development into the imago, which alone is offensive, we are satisfied. Eggs and larvae then, as many as you wish (pupae are too close to the final change to risk) provided there is no development of imagos.

Control of this mosquito then* by measures which allow of oviposition in their preferential breeding-places may be, in certain places will be, the preferential method to adopt.

Now by the use of fish, by oiling (not usually a method of election), and by emptying and refilling water containers at proper intervals of time, we can, in general, sufficiently control the production of *Stegomyia* and yet allow them access to their preferential breeding-places for oviposition. These methods then involve no risk of driving them to unusual breeding-places, the control of which may be difficult. Nay, even the removal of containers and the covering them so as to exclude access of mosquitos, methods very advisable for permanent work, can be used if other suitable breeding-places be provided accessible to them. The production of imagos from these breeding-places provided can be controlled, sometimes by fish or, as we know where we placed them, easily and absolutely by emptying them at the weekly inspection

It may be worth mentioning to you that a small amount of sugar added to the water is reported by Fielding to increase its attraction to this mosquito for oviposition, although her progeny do not thrive on it: an instance, and they are rare among the lower forms of life, in which the maternal instinct is at fault.

Very obviously, then, before systematic work against yellow fever is begun in West Africa a survey must be made to determine the

* This is a general rule applying to *Anopheles* no less than to *Stegomyia aegypti.*

limits there of both the normal and the compulsory breeding-places of its yellow fever vector, or vectors. If the compulsory breeding-places be beyond our ready control, we should, by some of the methods just given, try to arrange for the control of normal breeding, so as to produce little or no compulsory breeding, remembering always that less than a 100 per cent. reduction of *Stegomyia* will eliminate yellow fever.

If the normal breeding habits of this mosquito in West Africa generally are those implied by the report of Horn and Tytler and similar reports as obtaining at Salt Pond and Seccondee,* the elimination of yellow fever from that region would be, I think, impracticable by the methods we have used in the Americas.†

* Sir Rubert Boyce also notes having seen *Stegomyia* breeding in a pool on the mud-covered roof of a hut (*i.e.* 'puddle breeding') in West Africa. I think he does not state where.

† See footnote: page 500.